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Effect of Female Reproduction and Mate Choice on Sexual Size Dimorphism in the Northeast Treefrog *Hyla ussuriensis* (Anura: Hylidae) in China

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Abstract Sexual size dimorphism (SSD) plays a significant role in understanding the evolution of life history and mating behavior. In this study, we analyzed the morphological data from a treefrog, *Hyla ussuriensis*, in northeastern China and found that there are significant differences between males and females. Females that are larger in body size increase fecundity as the total number of eggs is positively correlated to female body size. Males are smaller in body size due to the mate choice by females based on the size dimorphism index (SVL mean of female divided by that of male) for the population, which may be an evolutionary stable strategy (ESS). SSD can be influenced not only through mate choice, but also reproductive behavior by analyzing the female reproduction output in the field. Our data are consistent with many previous studies, indicating that fecundity selection and sexual selection may be the common cause for sexual dimorphism in this species. Furthermore, there are no significant morphological differences between mated and unmated frogs of both sexes, which suggests that any frog can obtain a breeding chance when it matures. It further indicates that males may not affect female choice except by their snout-vent length (SVL) and body mass. It is, of course, possible that females adopt a mating strategy to mate with males whose SVL and body mass are smaller than paired females. Our research provides unequivocal evidence for effective female choice and information on the evolution of SSD in the production of anuran pairing patterns.

Keywords *Hyla ussuriensis*, morphology, mating pattern, fecundity selection, sexual selection

1. Introduction

Sexual dimorphism is widely known for most anuran species due to males having special mating behaviors such as calling and amplexus in the breeding season (Shine, 1979; Kupfer, 2007). Therefore, there is a need to describe mating patterns based on relative body size of partners in mating pairs (Woolbright, 1983; Gutiérrez and Lüddecke, 2002). In some anuran populations, males show asynchronous arrivals at the breeding site after hibernation, and so females may have a better opportunity to select their mating partners depending on such criteria as body size (Davies and Halliday, 1977; Howard and Kluge, 1985; Robertson, 1986; Lüddecke, 2001; Gutiérrez and Lüddecke, 2002; Liao and Lu, 2012) in non-random mating patterns (Woolbright, 1983). Consequently, mating patterns and reproductive output associated with morphological traits in frogs are crucial to understanding the origins of the sexual size dimorphism (SSD) phenomenon. Previous studies strongly suggest that SSD results from a balance of selective pressures differing in strength and direction between the sexes such as sexual selection (female choice or male-male contests for mating opportunities) (Robertson, 1986; Sullivan and Hinshaw, 1992) and fecundity selection (a selection leading to larger body size or body cavity in females) (Liao and Lu, 2009; Shi *et al*., 2011). These selection pressures affect male rather than female anurans in that females are larger than males (Wells, 2007). Commonly, the larger relative body length in females is a result of selection for higher fecundity in order to accommodate more eggs during the breeding season (Gibbons and McCarthy, 1986; Lemckert and Shine, 1993). Smaller body size in males is partially

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explained by loss of foraging time due to the energetic costs associated with male reproduction such as calling or chorusing to obtain greater mating chance or breeding success (Woolbright, 1983; Katsikaros and Shine, 1997).

Due to both its abundance in nature and sonorous calling sonority in breeding season, the genus *Hyla* has been the focus of mate choice and mate call research, which includes *H. regilla* (Whitney and Krebs, 1975), *H. marmorata* (Lee and Crump, 1981), *H. ebraccata* (Wells and Schwartz, 1984), *H. crucifer* (Forester and Czarnowsky, 1985), *H. cinerea* (Gerhardt, 1987), *H. chrysoscelis* (Morris, 1989), *H. arborea* (Marquez and Tejedo, 1990), *H. pseudopuma* (Crump and Townsend, 1990), *H. japonica* (Hirai and Matsui, 2000), *H. versicolor* (Schwartz *et al*., 2001) and *H. labialis* (Gutiérrez and Lüddecke, 2002). Despite these studies, detailed quantitative examination of the relation between morphometry and reproductive behavior ecology of the genus *Hyla* remains poorly understood.

The aim of this study was to describe the relationship of SSD and mating patterns in *H. ussuriensis*. We used field observations to address several questions: 1) Is sexual dimorphism pronounced in this species and what are the important morphological traits in its mate choice? 2) Are mating patterns related to the body sizes of males and females? 3) Can we recognize the influence of female fecundity traits and mate choice which are both related to body size?

2. Materials and Methods

2.1 Study species and area *Hyla ussuriensis*, Nikolsky, 1918 occurs in a large region from northeastern China to eastern Russia (Fei *et al*., 2009). It is a small frog with a prolonged breeding season (from early or mid-May to late July), compared to some other sympatric species such as *Rana dybowskii*, *R. amurensis* and *Bufo gargarizans*, and produces multiple broods during its reproductive season (Zhao *et al*., 2008). Detailed population life history traits and ecology information including the mating systems of *H. ussuriensis* in China still remain largely unstudied, and our knowledge of SSD in *Hyla* is scant (Fei *et al*., 2009; Zhao *et al*., 2008).

The field study was carried out in a valley close to Hailin City (Hengdaohezi Town; 44°07’ N, 129°06’ E, 460 m a. s. l.), Heilongjiang, northeastern China. *H. ussuriensis* was found spawning in some differently sized and shaped ponds surrounded by coniferous and broadleaved forests. We concentrated field work on a rectangular pond (35 × 30 m; Pond 1) and a circular pond (25 m in diameter; Pond 2) with a large quantity of frogs. On one night in June 2010 we counted ~200 males in Pond 2. Amplexus occured on pond banks or in the water, where males called mainly at night (19:00–24:00 h), with a peak calling period between 21:30–23:00 h. Males live in spawning fields from May to July every year in breeding season, and gravid females arrive unpredictably and enter the water for spawning (Zhao *et al*., 2008).

2.2 Sexual size dimorphism From May to July 2010, we simultaneously sampled adult specimens in the two ponds, including 99 unmated males, 13 unmated females and 19 mating pairs (Amplexus happened when they were caught). Twelve morphological variables were measured for SSD analysis: snout-vent length (SVL), head length (HL), head width (HW), snout length (SL), internasal distance (IND), interocular distance (IOD), eye diameter (ED), forelimb and hand length (FHL), forelimb width (FW), tibia length (TL), and hindlimb length (HL). All specimens were measured to the nearest 0.01 mm with vernier calipers. We measured each morphological variable three times per specimen for analysis, while holding the specimen against a flat surface. The body mass (BM) was measured with an OHAUS field balance to the nearest 0.01 g. All the captured frogs were marked by clipping the disc of the longest toe before released in the study area, so as to avoid repeating measurements on the same individuals. After toe clipping, antibacterial ointment was applied to the cut toe to prevent infection.

2.3 Female reproductive traits We captured 10 gravid females (the mated : unmated ratio was 1 : 1) at random for measuring SVL and BM, and then they were dissected to weigh the whole ovary. A part of ovary was weighed and the eggs were counted in order to compute the total number of eggs in the ovary by using the standard method of proportional mass divided by the whole mass (Shou *et al*., 2005). The eggs in sampled ovary were counted three times, and we took the mean as the number of eggs in every ovary.

2.4 Statistical analyses Statistical analyses were performed with SPSS software (Version 13.0). We used *t*-test, linear regression analysis, one-way analysis of variance (ANOVA), analysis of covariance (ANCOVA), and principal component analysis (PCA) to analyze the corresponding data. Prior to parametric analyses, data were tested for normality through Kolmogorove-Smirnov test and for homogeneity of variances through Bartlett’s test (at univariate level). Values are presented as mean ± standard error (SE). The significance level is set at 0.05.

3. Results

3.1 Sexual size dimorphism SSD was evident in the adults of *H. ussuriensis*. Among the samples captured for this study, the largest male and female were 43.38 and 47.71 mm SVL, respectively. The mean of SVL was significantly greater in females (40.87 ± 0.52 mm) than in males (36.60 ± 0.19 mm) (t = -7.671, P < 0.01) and the mean of BM was greater in females (5.68 ± 0.25 g) than in males (3.54 ± 0.05 g) (t = -8.254, P < 0.01) (Table 1).

SVL was significantly correlated with the other factors (all P < 0.05), so ANCOVA controlling for SVL found that females possessed larger HW, SL, ED, FHL, TL and HL than males with SVL being same as females (ANCOVA; HW, $F_{1, 149}$ = 5.711, P < 0.05; SL, $F_{1, 149}$ = 6.349, P < 0.05; ED, $F_{1, 149}$ = 8.446, P < 0.01; FHL, F = 10.275, P < 0.01; TL, $F_{1, 149}$ = 18.303, P < 0.01; HL, $F_{1, 149}$ = 30.014, P < 0.01) and males possessed a larger FW than females (ANCOVA; FW, $F_{1, 149}$ = 24.441, P < 0.01), while HL, INS and IOS did not show differences between the sexes (all P > 0.05) (Table 1). These results indicate that *H. ussuriensis* was grouped among sexually size-dimorphic species of frogs, with females being the larger sex, and the size dimorphism index (SDI: SVL mean of female divided by that of male; Woolbright, 1983) for the population was 1.12.

A principal component analysis resolved three components (with eigen-values > 1) from the twelve morphological variables accounting for 72.238% of the total variation in the original data. The first component (46.835% variance explained) had significantly positive loadings for SVL, HL, HW, FHL, TL, HL and BM, the second (16.528% variance explained) had significantly positive loadings for SL, IND, IOD and ED, and the third (8.875% variance explained) had significantly positive loadings for FW (Table 2). Males had lower scores on the first axis of a principal component analysis than females did (ANOVA, $F_{1, 149}$ = 197.223, P < 0.01), and females had lower scores than males on the third axis (ANOVA, $F_{1, 149}$ = 4.952, P < 0.05), but the score on the second axis did not differ significantly between the two sexes (ANOVA, $F_{1, 149}$ = 0.705, P = 0.403) (Figure 1).

3.2 Unmated and mated morphological characters We did not find differences in the twelve morphological variables between mated (n = 19) and unmated (n = 13) females, and the only differences between mated (n = 19) and unmated (n = 99) males were found in SL, IND, and ED. Mated males were significantly smaller in SL and IND, but bigger in ED than unmated males (SL, 3.61 *vs*. 3.94 mm, t = -2.524, P < 0.05; IND, 1.72 *vs*. 1.96 mm, t = -2.968, P < 0.01; ED, 4.78 *vs*. 4.38 mm, t = 3.514, P < 0.01). It seems that the males which have larger ED, smaller SL and IND have advantages over those possessing the opposite.

3.3 Morphological characters of amplexing frogs In the mating pairs of this test, the average SVL of mated males (36.64 ± 0.44 mm, ranging between 33.07−40.95 mm, n = 19) was significantly smaller than that of mated females (40.69 ± 0.61 mm, between 36.90−46.06 mm, n = 19) (t = -5.375, P < 0.01), and the average BM of mated males (3.57 ± 0.13 g, between 2.86−5.10 g, n = 19) was significantly smaller than mated females (5.58 ± 0.29 g, between 3.53−8.51 g, n = 19) (t = -6.256, P < 0.01)

Table 1 Descriptive statistics of morphological traits of *H. ussuriensis*. Data are expressed as mean ± SE and range (minimum–maximum), and compared using independent samples t-test (for SVL and BM, t values) or ANCOVA (for other morphological variables with SVL as the covariate, F values). Significant levels are indicated in the table, * P < 0.05, ** P < 0.01, *ns* > 0.05.

Variables	Males (n = 118)	Females (n = 32)	t or F values and P levels
Snout-vent length (mm)	36.60 ± 0.19 (28.59–43.38)	40.87 ± 0.52 (36.26–47.71)	-7.671** (M < F)
Body mass (g)	3.54 ± 0.05 (2.46–5.10)	5.68 ± 0.25 (2.96–9.31)	-8.254** (M < F)
Head length (mm)	10.39 ± 0.07 (8.11–12.55)	11.18 ± 0.15 (9.86–12.86)	0.116 (*ns*)
Head width (mm)	12.36 ± 0.09 (9.97–14.96)	13.71 ± 0.22 (11.32–16.77)	5.711* (M < F)
Snout length (mm)	3.89 ± 0.05 (2.75–5.76)	3.92 ± 0.09 (3.03–4.82)	6.349* (M < F)
Internasal distance (mm)	1.92 ± 0.03 (1.38–3.28)	1.92 ± 0.05 (1.39–2.58)	2.718 (*ns*)
Interocular distance (mm)	3.13 ± 0.04 (2.42–4.37)	3.34 ± 0.08 (2.16–4.23)	1.916 (*ns*)
Eye diameter (mm)	4.45 ± 0.06 (2.34–5.61)	5.15 ± 0.08 (4.36–6.10)	8.446** (M < F)
Forelimb and hand length (mm)	16.22 ± 0.14 (12.60–20.38)	18.83 ± 0.34 (14.34–22.74)	10.275** (M < F)
Forelimb width (mm)	3.19 ± 0.03 (2.17–4.10)	3.11 ± 0.08 (2.15–4.03)	24.441** (M > F)
Tibia length (mm)	15.81 ± 0.07 (13.99–18.20)	17.80 ± 0.27 (13.25–20.15)	18.303** (M < F)
Hindlimb length (mm)	52.04 ± 0.27 (45.32–58.55)	60.14 ± 0.98 (49.96–71.35)	30.014** (M < F)

Table 2 Loading of the first three axes of a principal component analysis on 12 variables of morphological traits of both sexes. Variables with the main contribution to each factor are shown in bold numbers.

Variables	Factor loading		
	PC1	PC2	PC3
Snout-vent length	**0.89**	-0.005	-0.07
Body mass	**0.735**	0.072	0.095
Head length	**0.697**	-0.426	0.222
Head width	0.395	**0.699**	0.161
Snout length	0.283	**0.656**	0.274
Internasal distance	0.46	**0.595**	-0.185
Interocular distance	0.513	**-0.662**	0.198
Eye diameter	**0.764**	0.198	-0.308
Forelimb and hand length	0.347	0.059	**0.812**
Forelimb width	**0.871**	-0.122	-0.089
Tibia length	**0.889**	-0.118	-0.241
Hindlimb length	**0.916**	-0.118	-0.082
Variance explained (%)	46.835	16.528	8.875

(Figure 2). We did not find a positive tendency for larger males to clasp larger females in SVL (Pearson correlation, $r^2 = 0.115$, $P > 0.05$, n = 19) and in BM (Pearson correlation, $r^2 = 0.142$, $P > 0.05$, n = 19) (Figure 2). The SDI of mating pairs was 1.11 ± 0.08 (ranging between 1.01−1.29), which was not significantly different within the population (1.12) ($P > 0.05$).

3.4 Female body size and fecundity Fecundity (the total number of eggs) of female *H. ussuriensis* was 435.40 ± 53.65 (254−736 eggs) during the breeding season, and there was no difference between mated and unmated females ($P > 0.05$, n = 10), so the data were combined. Fecundity was significantly and positively correlated with maternal SVL (Pearson correlation, $r^2 = 0.825$, $F_{1, 9} = 17.032$, $P < 0.01$; Figure 3) and BM (Pearson correlation, $r^2 = 0.926$, $F_{1, 9} = 48.163$, $P < 0.01$; Figure 3). The increasing body volume is, therefore, transformed into higher fecundity in larger females of *H. ussuriensis* and BM is more important than SVL.

4. Discussion

Sexual dimorphism is a widespread phenomenon and female-biased size dimorphism (in which males are smaller than females) occurs in 90% of anuran species (Shine, 1979; Howard, 1981), which is due to both natural and sexual selection (Katskaros and Shine, 1997). In this study, *H. ussuriensis* from China is similar to other *Hyla* frogs with females being larger than males (e. g., *H. squirella*, Buchanan, 1994; *H. japonica*, Hirai and Matsui, 2000; *H. labialis*, Gutiérrez and Lüddecke, 2002; *H. annectans chuanxiensis*, Liao and Lu, 2010), meaning that females have larger SVL, heavier BM, and longer forelimbs and hind limbs than males, with males having wider forelimbs than females after accounting for SVL. These differences in local morphological characters between the two sexes were validated in principal component analysis (PCA) (Figure 1). Our data show that female size (SVL and BM) is an important factor which influences absolute fecundity of *H. ussuriensis*, that is, larger females produce more eggs (Figure 3). This offers strong evidence to support the hypothesis that selection for higher fecundity results in the evolution of a longer trunk (Woolbright, 1983; Vargas-Salinas, 2006). At the same time, forelimb and hindlimb were more important in both sexes of frogs because of the method of saltatorial locomotion (Hirai and Matsui, 2001). Furthermore, longer limbs can help females in supporting more weight during the gravid period and carrying mating males, as well as improving swimming and jumping to escape from predators in the field (Shou *et al*., 2005).

In the population of *H. ussuriensis* with a prolonged reproductive season and a male-biased sex ratio, we tested the hypothesis that morphological characters and fecundity possessed no differences between mating and unmating females. In other words, all the mature females could have a chance to amplex during the breeding season and the size of a mated male depended on the females' mate choice (Marquez and Tejedo, 1990; Schwartz *et al*., 2001; Sullivan *et al*., 1995). In the previous study, small males actively court small females whereas

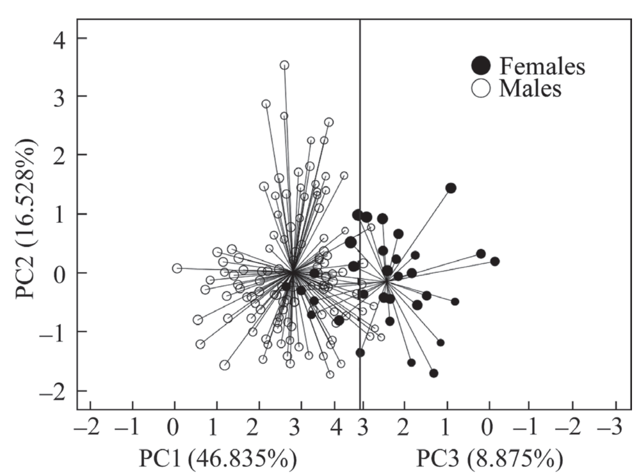

Figure 1 The space defined by the first three axes of a principal component analysis (PCA) based on 12 morphological variables of *H. ussuriensis*. Center symbols show the score values of both sexes on the three axes, respectively.

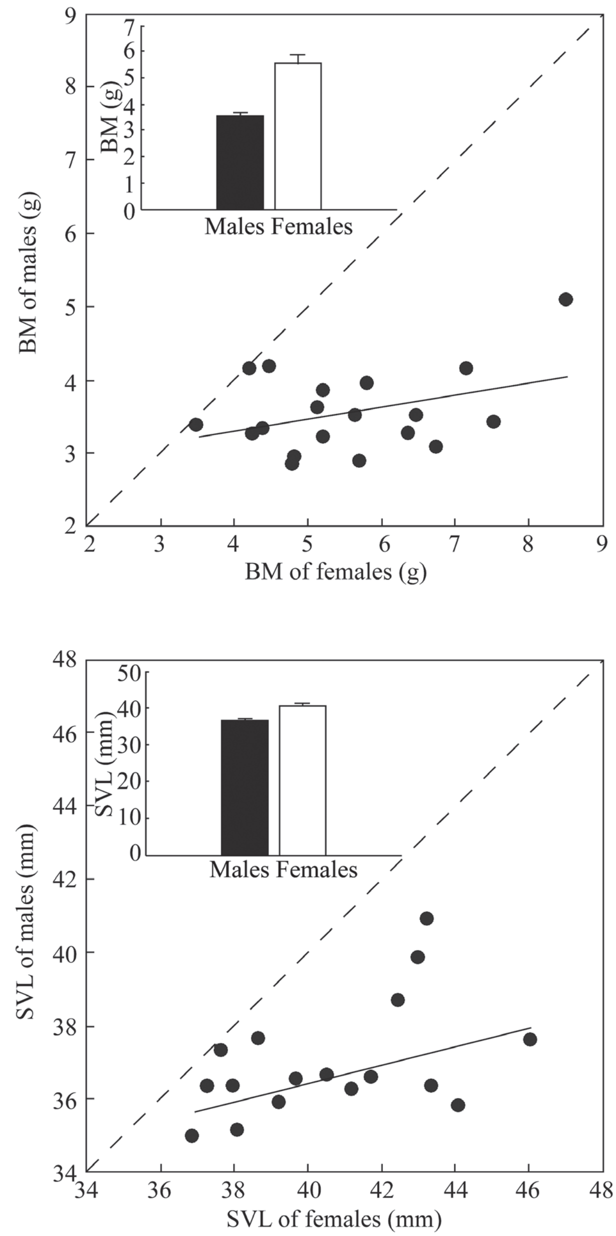

Figure 2 Relationship between SVL (mm) and BM (g) of females and males of *H. ussuriensis* amplexus. Solid lines: Regression lines; Dash lines: Diagonal lines.

large males court large females, or all males court large females, but only large males are able to obtain a successful mating (Halliday, 1983; Shine *et al*., 2001). But the size-assortative mating choice mode is not in *H. ussuriensis* because we do not find a positive relation of *H. ussuriensis* amplexus in SVL and BM (Figure 2), though fertilization success appears to be greater when partners are optimally paired (Davies and Halliday, 1977). Females always mate with those particular males whose SVL is smaller and proportion with hers closest to SDI (1.12). It seemed that in other species of frogs large males have no mating advantage (Sullivan, 1983; Lüddecke, 2001), though the possible advantage of males with larger SVL in copulatory behavior has been discussed several times (Shine, 1979; Katsikaros and Shine, 1997; Liao and Lu, 2011a). Therefore, we are sure that male size does not affect mating success not only in *H. ussuriensis*, but also in *H. versicolor*, *H. crucifer*, *H. regilla* (Fellers, 1979) and *Rhacophorus omeimontis* (Liao and Lu, 2011b). Females preferred males which have larger ED, smaller SL and IND only based on their own favor, so there is no significant SSD in these traits as it is not important in male-male contests. Wider forelimbs could be selected for males because they have a better ability to hold onto female in amplexus, and this sexual selection may result in SSD (Wells, 1977; Berven, 1981; Liao *et al*., 2012).

In our study, the morphological traits of males were not key in the mate choice expecting for their smaller

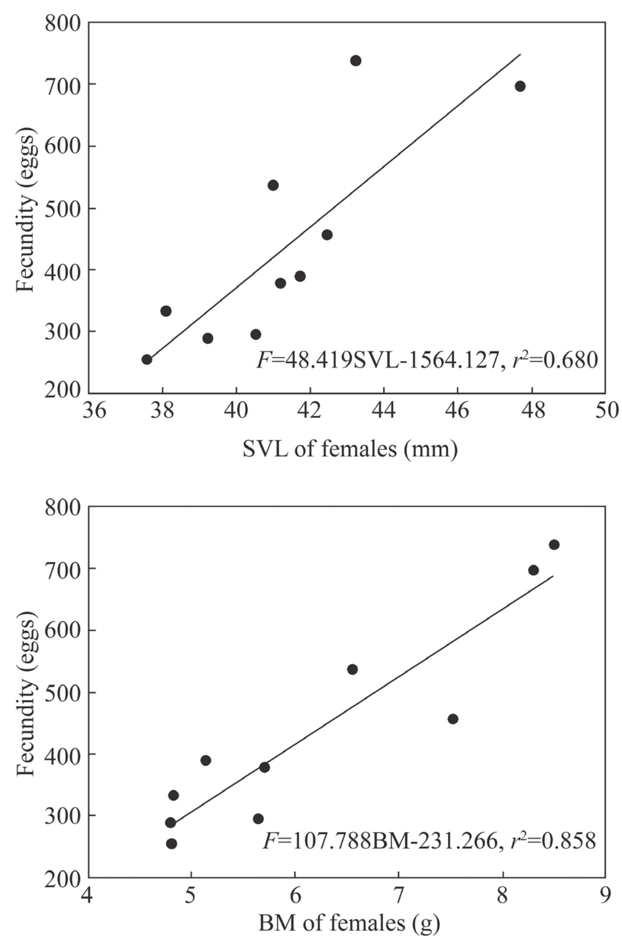

Figure 3 Linear regression of fecundity (the total number of eggs) against SVL(mm) and BM (g) of females in *H. ussuriensis*. The regression equation is indicated in the Figure. F: Fecundity. See text for statistical analyses.

body size and mass relative to females, so other traits such as chorusing will be more important. During the breeding season, the sound of chorusing males leads females to the pond (Wells, 1977), and leads to the mating model by which females approach calling males to mate (Searcy and Andersson, 1986; Höbel and Gerhardt, 2003). Acoustic signaling is, therefore, the most important form of communication in anuran amphibians (Pröhl, 2003; Wei *et al*., 2011), particularly, its dominant frequency and call duration (Doty and Welch, 2001), which vary with male body length and weight (Robertson, 1986; Gerhardt, 1994) and play a role in female mate selectivity (Nunes *et al*., 2007). All of this detailed knowledge including longevity, growth rate, age at sexual maturity and mate success is essential for revealing the mechanisms underlying the evolution of SSD (Andrews and Stamps, 1994; Thomas and Georg, 2005; Ma and Lu, 2009).

In conclusion, *H. ussuriensis* presents size dimorphism between the sexes and SSD can be influenced by female fecundity and mate choice. On one hand, characteristics that allow high reproductive performance are selected in females, resulting in larger bodies. On the other hand, characteristics that obtain more chances to copulate are selected in males with specific and smaller body sizes (based on the population SDI). They work together and lead to sexual dimorphism in *H. ussuriensis*. Because adult body size is indirectly linked to many, if not most, life-history characters, a more holistic approach of SSD will be needed in the future (Arak, 1988).

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